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Title page

Prioritization of habitat patches for landscape connectivity conservation differs between
least-cost and resistance distances

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Abstract

Context. Methods quantifying habitat patch importance for maintaining habitat network connectivity have been emphasized in helping to prioritize conservation actions. Functional connectivity is accepted as depending on landscape resistance, and several measures of functional inter-patch distance have been designed. However, how the inter-patch distance, i.e. based on least-cost path or multiple paths, influences the identification of key habitat patches has not been explored.

Objectives. We compared the prioritization of habitat patches according to least-cost distance (LCD) and resistance distance (RD), using common binary and probabilistic connectivity metrics.

Methods. Our comparison was based on a generic functional group of forest mammals with different dispersal distances, and was applied to two landscapes differing in their spatial extent and fragmentation level.

Results. We found that habitat patch prioritization did not depend on distance type when considering the role of patch as contributing to dispersal fluxes. However, the role of patch as a connector facilitating dispersal might be overestimated by LCD-based indices compared with RD for short- and medium-distance dispersal. In particular, when prioritization was based on dispersal probability, the consideration of alternatives routes identified the connectors that probably provided functional connectivity for species in the long term.

However, the use of LCD might help identify landscape areas that need critical restoration to improve individual dispersal.

Conclusions. Our results provide new insights about the way that inter-patch distance is viewed changes the evaluation of functional connectivity. Accordingly, prioritization

- 24 methods should be carefully selected according to assumptions about population
- 25 functioning and conservation aims.
- 26
- 27 **Keywords.** habitat network connectivity; graph theory; connectivity indices; least-cost path;
- 28 resistance distance; circuit theory; landscape resistance; species dispersal; landscape
- 29 fragmentation; habitat patch importance

Introduction

Landscape connectivity is accepted as being crucial for biodiversity conservation, because land-use changes and habitat fragmentation per se can dramatically damage species' habitats and species' dispersal. The way a landscape allows or impedes movement of species determines the fluxes of individuals or genes that are exchanged between habitat patches, which help to maintain populations and metapopulations (Verbeylen et al. 2003; Stevens et al. 2006; Amos et al. 2014). Recently, applications of graph theory to landscape ecology have shown potential for quantifying the connectivity of landscape for a species or species group by focusing on the role of habitat patches and dispersal linkages between them (Pascual-Hortal and Saura 2006; McRae and Beier 2007; Pinto and Keitt 2009; Rayfield et al. 2011). In particular, researchers have developed methods to identify the most important habitat patches for maintaining the global connectivity of habitat networks (Pascual-Hortal and Saura 2006; Urban et al. 2009; Bodin and Saura 2010; Saura and Rubio 2010; Ernst 2014). These prioritization methods are thought to be particularly useful for conservation biologists and landscape managers: they can guide the location of future finer-scale studies and help to define conservation, restoration or mitigation measures that should favour a better (spatial) allocation of funds and efforts to protect biodiversity (Zetterberg et al. 2010; Foltete et al. 2014; Gurrutxaga and Saura 2014).

Habitat patch prioritization based on landscape graphs uses connectivity indices that quantify the importance of each habitat patch for habitat network connectivity, taking into account its position in the habitat network with, for example, centrality indices (e.g. Estrada and Bodin 2008). But, connectivity indices generally consider both the position and the quality (or quantity) of available habitat such as the Integral Index of Connectivity (IIC) and

the Probability of Connectivity index (PC) (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Rubio 2010). These connectivity indices make a compromise between the effects of landscape composition and landscape structure on species presence, a question still debated in the literature (Didham et al. 2012). Different attributes of habitat patches can be used to consider habitat patch quality: this can depend on species requirements, but more often on the information available, often justifying the use of proxies of habitat patch quality calculated from landscape maps such as patch area, patch interior area or level of anthropogenization. How well one habitat patch is linked to the rest of the habitat network depends on the distance between this habitat patch and the other patches, but the way in which the method used to calculate this distance affects the degree of connectivity of habitat patches remains unclear. Traditionally in graph theory, distance between habitat patches was just the topological distance, i.e. Euclidean distance, but in this last decade many studies on animal dispersal movement have shown that Euclidean distance is not realistic because it does not integrate the difficulty or mortality encountered by a species moving through a landscape mosaic (Adriaensen et al. 2003; Belisle 2005). Many efforts have been made to integrate landscape resistance more fully with species movement, and two methods are now widely used to quantify the distance a species has to travel to disperse between habitat patches.

The classical least-cost path is based on friction maps reflecting the difficulty for a species to move between two source patches (Adriaensen et al. 2003). A species accumulates a cost with increasing distance from source patches, depending on its dispersal capacities and specific habitat encountered. The least-cost distance (LCD) is the accumulated cost distance of the most likely route an individual would take to move between the two habitat patches considered, i.e. the least-cost path (LCP). However, LCP implies that species

77 know the optimal path to get to a new habitat patch, and a major criticism is that it does not
78 take into account the existence of other optimal paths, whereas species generally use
79 random or alternative dispersal routes depending on individual behaviour (Belisle 2005).
80 Nevertheless, LCD itself indicates the minimum distance separating the individual habitat
81 patches and so the reachability of habitat for species. LCD is therefore now preferred to
82 Euclidean distance for parameterizing connectivity indices prioritizing habitat patch
83 importance (Zetterberg et al. 2010; Gurrutxaga et al. 2011; Clauzel et al. 2013). A recent
84 significant advance in quantifying resistance distance separating habitat patches was
85 provided by circuit theory, which takes into account random movement paths and path
86 redundancy (McRae and Beier 2007; McRae et al. 2008). An electric current flowing through
87 landscape resistance maps represents species dispersal flux at each point of the landscape:
88 all the alternative paths between two habitat patches are used to calculate resistance
89 distance (RD), which represents the effective distance separating the two habitat patches for
90 a species. The more alternative paths there are, the shorter RD is compared to LCD. RD has
91 been particularly widely used in genetic studies to evaluate functional landscape
92 connectivity by correlating RD to genetic distance between population patches (Amos et al.
93 2014; Marrotte et al. 2014), and current maps are considered to identify dispersal corridors
94 well (Roever et al. 2013). Some studies have used both LCD and RD (or resulting maps) to
95 find out which is the better predictor of species movement corridors (Poor et al. 2012;
96 LaPoint et al. 2013) or how they change with cost map parameterization (Koen et al. 2012).
97 One recent study (Ayram et al. 2014) used both LCD and circuit theory to identify important
98 landscape elements: IIC index was based on LCD to determine key habitat patches, and
99 current maps were used to locate corridors for two mammal species. However, to our
100 knowledge, how LCD and RD influence patch importance and the identification of key

elements maintaining habitat network connectivity has never been studied. It remains unclear whether the modelling of alternative paths, which is very time-consuming, is really required to identify key elements for habitat connectivity, or whether the modelling of the one best path, which is faster, is sufficient to approximate habitat patch importance adequately.

In this article, we compare the prioritization of habitat patches from graph models based on LCP and from graph models based on RD. We used binary and probabilistic connectivity indices, i.e. Betweenness Centrality (BC), patch importance based on Integral Index of Connectivity (dIIC) and based on Probability of Connectivity (dPC), in order to provide support in the use of the most commonly employed connectivity indices in conservation studies. We hypothesized that the identification of key habitat patches would tend to agree with increasing dispersal distance, but that identification could remain different in certain cases, particularly when the probability of dispersal was considered, since RD integrates multiple paths unlike LCD. We go on to discuss ecological hypotheses that might explain these differences. Our comparison is based on two real landscapes (e.g. Koen et al. 2010; Koen et al. 2012) ranging in habitat cover, fragmentation level, and spatial extent to verify consistency of relationship with landscape structure. Habitat patch prioritization focused on forest mammal species with different dispersal distances using a generic approach and following a conservation perspective, not a restoration or mitigation perspective. In this case, habitat patch prioritization aims to evaluate the importance of each habitat patch for maintaining the global connectivity of the habitat network for the species.

Material and Methods

Study area and land cover map

Two study cases were selected in the South of France (43°01' – 45°07' N and 4°13' – 7°43' E). The first study case, hereafter named "Region", followed the administrative boundaries of Region PACA, excluding isolated parts (e.g. Mediterranean islands) and encompassed about 31700 km². Region was mainly covered by forests (38%), other semi-natural and natural areas (35%), agricultural areas (17%) and artificial areas (7%); other areas were wetlands and water bodies (3%). A second landscape hereafter named "Sub-region" was a sub-area of about 7090 km², and contained strong human-created barriers. Sub-region was affected by a higher level of anthropogenization than Region, with a lower cover of forests and other semi-natural and natural areas (27% and 26% respectively), and a higher cover of agricultural areas and artificial areas (31% and 11% respectively). Other areas were wetlands and water bodies (3%). The study area was bordered by the Alps at the East, anthropogenized areas at the West and the Mediterranean Sea at the South. Landscape habitats came from the map ocsol2006 of Crige PACA (www.crige-paca.org), an adaptation of the CORINE land cover nomenclature of the European Environmental Agency (<http://www.eea.europa.eu/data-and-maps>) for French Mediterranean landscapes with a smaller spatial resolution. The land cover map identified 42 types of landscape features, including natural and human-dominated lands, highways and major railways, with a minimal mapping unit varying from 0.5 to 2.5 ha.

Functional group approach

We focused on generalist forest mammal species using a generic approach for our connectivity models, because these species depend on a well-defined habitat and are known to be sensitive to landscape features of interest for land managers, such as transportation infrastructures, and urban and other anthropogenized areas. We collected scientific literature on forest mammal species and consulted studies using a generic forest species approach (Verbeylen et al. 2003; Watts et al. 2010; Garcia-Feced et al. 2011; Gurrutxaga et al. 2011; Gimona et al. 2012) to determine the resistance of landscape features to animal movement. The attribution of cost values to landscape features is still under debate (Zeller et al. 2012; Mateo-Sanchez et al. 2015) and would be based on ad hoc data, i.e. showing species dispersal movement (pathways data), in the ideal but very uncommon case. Consequently, we focused on studies that conducted sensitivity analyses to model connectivity between forest habitat patches, such as that of Verbeylen et al. (2003), who tested a range of cost values and cost classes to find the best combination explaining the presence of forest species in forest habitat patches. Our review caused the original land cover map to turn into a landscape resistance map with five cost classes: 1 for forest areas (species habitat), 10 for less open areas with trees (or potential feeding-seed trees), 300 for more open areas including shrubs or gardens, 800 for areas with low vegetation such as agricultural lands, and 1000 for landscape features that most impeded animal movement such as highways, buildings and permanent snow. We then rasterized the cost map at a 100 m pixel size to reduce calculation time for analysis (McRae et al. 2008). Habitat patches were defined as entirely covered by forest, up to the upper tree-line at 2100 m a.s.l. and with a surface area of at least 10 ha. We kept 621 forest habitat patches for Sub-region and 2482 forest habitat patches for Region. GIS calculations were performed with ArcGis 10 (ESRI®).

168

169 **Least-cost distance and resistance distance**

170 Linkages were modelled between habitat patches using a maximum distance according to
171 species dispersal capacities and the extent of the study area. For connectivity analyses (see
172 below), we used a range of distances rather than only one, enabling us to take into account
173 information disparity in the literature and variation in species dispersal distance (e.g.
174 juvenile dispersal, adult dispersal, long-distance dispersal events). Most importantly, this
175 enabled us to analyse how our connectivity models changed with dispersal distance and so
176 to what extent LCP-based prioritization is correlated to RD-based prioritization. Our review
177 prompted us to use the following dispersal distances (edge-to-edge of habitat patches): 200
178 m, 700 m, 1000 m, 4000 m, 6000 m, 10 km, 15 km, 20 km and 25 km. Our connectivity
179 models thus considered a range of dispersal distances ranging from 200 m to 25 km,
180 enabling us to consider short-, medium- and long-distance dispersal of forest mammal
181 species. The maximum dispersal distance of 25 km yielded 898 linkages for Sub-region and
182 3399 for Region. In this article, dispersal distance was in kilometres but it was actually a cost
183 distance: in the analyses, dispersal distance was multiplied by the median value of the cost
184 raster to reflect the cost of the path travelled by the species (e.g. Gurrutxaga et al. 2011). A
185 species moves a larger geographical distance through permeable landscape features than
186 through landscape features with high resistance. Dispersal distances stated in the literature
187 often result from straight-line distance calculations between pre- and post-dispersal habitat
188 patches (e.g. Wauters et al. 2010), whereas species had actually moved through different
189 landscape features along a much longer non-linear path (Rowcliffe et al. 2012).

We used Linkage Mapper 1.0.3 (McRae and Kavanagh 2011), a free tool box implemented in ArcGis, to calculate LCD between each pair of habitat patches: LCD is the accumulated cost distance of the most likely route an individual would take to move between the two habitat patches considered. Only direct linkages between habitat patches were considered to construct the habitat network model (see below). Using circuit theory with Circuitscape (McRae et al. 2008; Shah and McRae 2008), we then calculated RD between each pair of habitat patches (pairwise mode and connection option with eight neighbours). Calculating RD was particularly time-consuming with a large numbers of patches and linkages, because all the paths between two habitat patches have to be considered. The resistance to current flow was therefore computed on the entire landscape area, and for each pair of habitat patches. We were not interested in the precise location of dispersal corridors, but in a measure of distance between habitat patches that took into account alternative paths. Hence to calculate RD, we restricted the current flow analysis to a corridor surrounding the least-cost path determined previously by applying a cut-off of 700 m (cost width of corridor) and using an extension of Linkage Mapper that applied Circuitscape in this specific way (McRae 2012). Consequently, all alternative paths not exceeding 700 m from the least-cost path were kept to compute RD between a pair of patches. When landscape impedes species movement, least-cost corridors are narrow and there are few alternative paths between patches for species, so RD approximates to or equals LCD, but when landscape is favourable to species movement, least-cost corridors are wide and there are many alternative paths, making RD strongly shorter than LCD. In this case, individuals have more chance of reaching the other habitat patch. We also calculated RD for a corridor cut-off of 4000 m in order to verify how corridor cut-off could change the estimation of habitat patch importance. Habitat patch importance for the two cut-offs was

closely correlated: Spearman's rho was at least 0.92, but generally above 0.94 for both Region and Sub-region. We therefore kept RD based on a corridor cut-off of 700 m in what follows. The calculation of LCD and RD for Sub-region was applied to the spatial extent of Region (acting as a buffer, see Koen et al. 2010), to make the estimation of distance independent of artificial boundary (only present at the North of Sub-region, see Material and Methods).

Connectivity indices for evaluating habitat patch importance

The habitat network model was composed of nodes representing habitat patches characterized by their surface area, and of direct links representing linkages between habitat patches characterized by their travel cost (LCD or RD). A set of connectivity indices was calculated from the habitat network model with the free software Conefor 2.6 (Saura and Torne 2009) in order to quantify the relative importance of habitat patches for global network connectivity. Here we present the different indices used only briefly, all being detailed and their use justified in an abundant literature. Moreover, our aim was not to investigate the differences between connectivity indices (see Bodin and Saura 2010; Baranyi et al. 2011), but to compare habitat patch ranking according to LCD-based linkages and RD-based linkages for different connectivity indices currently used in the conservation biology literature. A path or linkage is always the direct dispersal between two habitat patches (i.e. with no other intermediate habitat patch), whereas the term pathway is used with a general meaning, i.e. dispersal ways in habitat network (direct or indirect). All connectivity indices used in this study are given in Table 1. Betweenness Centrality (BC) considers the number of shortest pathways between all pair of nodes that go through a particular node, and so does

not consider the node attribute (surface area). $dIIC_{flux}$ ($dIICf$), $dIIC_{connector}$ ($dIICc$), dPC_{flux} ($dPCf$) and $dPC_{connector}$ ($dPCc$) are fractions resulting from the decomposition of the node importance value ($dIIC$, dPC) based on Integral Index of Connectivity (IIC) and on Probability of Connectivity (PC) respectively (Table 1). Flux fraction of a particular node ($dIICf$, $dPCf$) quantifies the amount of dispersal flux that occurs between the node and the rest of the network, and depends on the node attribute and the shortest pathways that link the node to the network (topological position). Connector fraction of a particular node ($dIICc$, $dPCc$) exists only if the shortest pathways between other nodes pass through the node, and so depends only on topological position; it quantifies the importance of the node as a stepping-stone for dispersal, i.e. facilitating dispersal between excessively far nodes. We also computed the last fraction of node importance, the intra fraction ($dIICi$, $dPCi$) of a particular node, which depends only on the node attribute, and so has the same value whether the node is connected or not (see Saura and Rubio 2010). Investigating how the fractions connector and flux change with linkage type helped us to make a better evaluation of how connectivity models impact the importance of patch, and so support more precise recommendations for the use of prioritization methods. All indices were calculated for the nine dispersal distances and for the two landscapes. Dispersal distance acted as a threshold determining the presence of a link between two nodes in the case of binary indices (BC, $dIICf$, $dIICc$). In the case of probabilistic indices ($dPCf$, $dPCc$), dispersal distance determined the median probability associated with a link, defining the distance-decay constant α in the relation $p_{ij} = e^{-\alpha d_{ij}}$ (Urban and Keitt 2001; Saura and Pascual-Hortal 2007) where p_{ij} is the probability of dispersal between nodes i and j , and d_{ij} their distance (LCD or RD). BC, $dIICf$, $dIICc$, $dPCf$ and $dPCc$ have been shown to be non-redundant indicators of patch contribution in the maintaining of habitat network connectivity (Baranyi et al. 2011). Finally, we summed

node importance values for each fraction flux, connector and intra over all the nodes, and then calculated the percentage of each sum relative to the total node importance values (Saura and Rubio 2010). This percentage was calculated for each dispersal distance in order to examine how habitat network connectivity (flux fraction and connector fraction of habitat network) changes according to LCD-based or RD-based indices. Connector fraction peaks when key stepping-stones become connected to habitat network, and flux fraction increases with connection of large habitat patches (high quality patches) and with the number of alternative pathways in the habitat network (Saura and Rubio 2010). We also calculated BC(IIC) and BC(PC), which are modifications of BC integrating properties of IIC and PC and are argued to be further useful indices (Bodin and Saura 2010), but we do not present the results for these indices since they were very closely correlated to dIICc and dPCc for both LCD and RD linkages (Spearman's rho was at least 0.91) and showed the same correlation pattern as dIICc and dPCc (see below).

Comparison of LCD- and RD-based connectivity indices

The higher the value of connectivity index, the greater the importance of the node for global habitat network connectivity. For each connectivity index and each dispersal distance, we compared node importance given by the LCD-based index to node importance given by the RD-based index by ranking importance values and applying rank correlation with Spearman's coefficient rho, which allowed control for extreme values and non-linear relationships. Only a limited number of habitat patches have a significant importance for the persistence of overall connectivity, and financial resources for nature conservation are generally restricted (e.g. Bodin and Saura 2010; Zetterberg et al. 2010; Gurrutxaga et al. 2011). Thus, after

examining quantile distributions of index values, we kept only the 25 top-ranked habitat patches according to the LCD-based index and the RD-based index in further analyses, focusing on Sub-region, since results were closely similar at Region (see Supporting Material). We identified in which cases habitat patches were top-ranked only by the LCD-based index, only by the RD-based index and by both indices, and projected them on the habitat network map.

Results

Habitat patch prioritization according to LCD-based and RD-based

indices

Correlations between LCD-based indices and RD-based indices increased with dispersal distance for the two landscapes Sub-region and Region (Fig. 1 and Fig. S1). Correlations strongly increased from 200 m to 1000 m, then increased more slowly up to 4000 m, where Spearman's rho generally exceeded 0.9, and were stable further away. For the smallest dispersal distances, a large part of LCD-based linkages was not established between habitat patches since linkage length exceeded the dispersal distance considered: 37.1%, 17.4%, 13.5% and 2.9% of LCD-based linkages exceeded dispersal distance at 200 m, 700 m, 1000 m and 4000 m for Sub-region respectively (27.1%, 12.3%, 8.8%, 1.7% for Region respectively). As expected, there were only a few cases where RD-based linkages exceeded the dispersal distance (2.6% and 1.6% at 200 m for Sub-region and Region respectively). Hence habitat network models based on LCD and on RD strongly differed for small dispersal distances,

while they became more similar with increasing dispersal distances. The sum of node importances reflected this convergence with increasing dispersal distances (Fig. 2 and Fig. S2). Differences persisted at slightly longer dispersal distances for probabilistic indices than for binary indices, particularly for connector fraction (Figs 1 and 2). The sum of node importances for Sub-region showed that dPCc peaked at 200 m and was rather stable from 1000 m when based on RD, but strongly decreased after 4000 m when based on LCD. By contrast, values of dIICc were similar at least from 4000 m for both distance types (same results for Region, Fig. S2). This difference occurred because for probabilistic indices, dispersal probability associated with the linkages increased much more rapidly when considering RD and alternative paths than when considering LCP and only one optimal path.

Figure 1. Correlation between habitat patch importance according to LCD-based and RD-based index for binary (a) and probabilistic indices (b) for Sub-region. Intra fraction (i), flux fraction (f) and connector fraction (f) are the partition of node importance dIIC and dPC. Tick marks without labels are 700, 1000 and 6000 m respectively.

Figure 2. Relative contribution of each fraction intra (i), flux (f), connector (c) to habitat network connectivity according to LCD-based and RD-based indices for Sub-region. Each fraction represents the contribution of all individual habitat patches relative to their total importance for maintaining connectivity. Tick marks without labels are 700, 1000 and 6000 m respectively.

The comparison of habitat patch ranking according to importance values given by LCD-based indices and by RD-based indices showed strong similarities (Fig. 3 and Fig. S3) that could be explained by strong correlations between connectivity indices for a type of linkages. First, the comparison of habitat patch ranking followed the same pattern for dIICf and dPCf, and their correlations were above 0.92 both for LCD-based and RD-based indices for Sub-region (>0.9 for Region). Second, comparison showed the same pattern for dIICc and BC, and their correlation was above 0.91 for both LCD-based and RD-based indices for Sub-region (>0.92 for LCD-based indices and >0.87 for RD-based indices for Region). The pattern was

slightly different for dPCc and its correlation with other indices was lower (<0.8 in all cases). Indeed, three different cases occurred concerning habitat patch prioritization. Firstly, LCD-based indices gave a much higher importance to habitat patches than RD-based indices. The most illustrative case occurred when habitat patches had a moderate importance with LCD-based indices and had null importance (rank 1) with RD-based indices (see Fig. 3). Secondly, RD-based indices gave a much higher importance to habitat patches than LCD-based indices. The most illustrative case occurred when habitat patches had a moderate-to-high importance with RD-based indices and null importance with LCD-based indices. Thirdly, LCD-based and RD-based indices attributed closely similar importance value to habitat patches.

Figure 3. Habitat patch importance rank according to LCD-based versus RD-based indices for Sub-region. Minimal rank is attributed when several importance values are the same. Other dispersal distances are not shown. Circles illustrate some cases where prioritization strongly differed.

Identification of top-ranked habitat patches

We focused on the 25 habitat patches with the greatest contribution for maintaining global habitat network connectivity at Sub-region level and projected the three different cases on the habitat network map. From the 700-m dispersal distance, almost the same habitat patches were identified by IICf and PCf based on LCD or RD linkages, whereas they strongly differed until the 1000-m dispersal distance for BC and IICc (Figs 4 and 5). The prioritization of habitat patches by dPCc remained divergent even when considering large dispersal distances, and only about 50% of top-ranked habitat patches were identified by both index types whatever the distance (Fig. 4). This means that when connectivity indices were weighted by patch attributes (IICf and PCf), linkage type had very little importance for patch

prioritization in our study, but it had high importance when connectivity indices were based only on dispersal distance for short- and medium-distance dispersers (BC and IICc) or when they were based on dispersal probability (dPCc). In certain cases for binary indices, habitat patches were top-ranked by the RD-based index, whereas the LCD-based index gave them a null importance as habitat patches were at one end or totally isolated in the LCD-based habitat network (see arrow 1 on Fig. 5). However, in other cases, habitat patches were top-ranked only by the RD-based index, although they might have been expected to be top-ranked also by the LCD-based index (arrows 2, Fig. 5): the loss of these habitat patches seriously affected dispersal between group of patches and the rest of the LCD-based habitat network for short-distance and medium-distance dispersers, because there was no alternative pathway, or only much longer pathways with many intermediate steps. LCD-based indices evaluated other habitat patches as being more important for network connectivity (e.g. arrows 3 on Fig. 5), their loss causing the total isolation of a large part of the habitat network. However, RD linkages showed several alternative pathways with an equivalent or smaller number of steps, thus providing other connections with the rest of the habitat network. Consequently, LCD-based indices tended to overestimate the role of certain habitat patches compared with RD-based indices, because they seemed to act as key connectors for maintaining habitat network connectivity whereas alternative pathways existed (see Figs 5 and 6). This resulted in a decrease in the importance of the other habitat patches identified as key-elements by RD-based indices.

Figure 4. Among the 25 top-ranked habitat patches, number of patches identified commonly by LCD-based and RD-based indices.

Figure 5. Map showing the 25 top-ranked habitat patches according to dIICc for a maximum dispersal distance of 1000 m. Top-ranked patches only by RD-based (green), only by LCD-based (orange) and by both indices (lilac), other habitat patches

in grey. Difference between LCD-based rank and RD-based rank in bold. Linkages are established when $RD \leq 1000$ m (red and green); and in fewer cases when $LCD \leq 1000$ m (red).

LCD linkages were up to 74 times longer than RD linkages, so habitat network based on LCD strongly differed from habitat network based on RD for small and medium dispersal distances, dispersal probability associated with LCD being very small compared with RD (Fig. 6). As dispersal capacity increased, dispersal probability increased strongly for LCD linkages, and the habitat patches identified only by RD-based dPCc tended to be identified also by LCD-based dPCc, i.e. the disparity of patch ranking for these patches decreased (compare top-ranked patches by RD-based dPCc between Figs 6 and 7). However, the disparity of patch ranking increased for the patches identified only by LCD-based dPCc (compare Figs 6 and 7): they occurred in landscape areas that remained poorly connected by LCD linkages at a large distance (Fig. 7a), whereas these areas became well connected by RD linkages (Fig. 7b). There were alternative pathways with high dispersal probabilities since large corridors and different paths between patches could be used by individuals to disperse (Fig. S4).

Figure 6. Maps showing the 25 top-ranked habitat patches according to dPCc for the 6000-m median dispersal distance.

LCD-based (a) and RD-based linkages (b) are represented according to their dispersal probability. See Fig. 5 for other details.

Figure 7. Maps showing the 25 top-ranked habitat patches according to dPCc for the 25-km median dispersal distance.

LCD-based (a) and RD-based linkages (b) are represented according to their dispersal probability. See Fig. 5 for other details.

Discussion

We report evidence that there was strong divergence between habitat patch prioritization based on linkage reflecting the least-cost path and that based on linkage reflecting multiple paths, depending on the type of connectivity indices and species dispersal distance. The

same patterns of prioritization occurred for both landscapes Region and Sub-region, which strongly differed in terms of spatial extent, landscape composition and fragmentation. This suggests that the correlation patterns we found in this study may not depend on landscape extent and landscape structure. However, further investigations are needed to measure to what extent the correlation between LCP-based prioritization and RD-based prioritization will follow the same pattern when landscape structure changes. Prioritization indices are presented as tools helping practitioners to orientate field conservation measures by the use of available knowledge about dispersal capacities and species requirements (Galpern et al. 2011), since it is not (or only rarely) possible to obtain robust data on real species fluxes between habitat patches at large scales. Hence, the use of prioritization indices and least-cost corridors or current maps identifying potential key landscape areas is an important advance for landscape and species conservation management (Beier et al. 2011; Lawler et al. 2013; Ayram et al. 2014). LCD and RD are methods with marked conceptual differences, and we showed that the way they influence prioritization of landscape features is not trivial.

LCD-based and RD-based indices identified almost the same habitat patches even for short dispersal (from 700 m) when considering the role of patches as providers (or receivers) of individual fluxes. Habitat patch attribute weighted the influence of distance type, and when large habitat patches were well connected to the habitat network (mean patch area was 178 ha for Sub-region but 3140 ha for the 25 top-ranked habitat patches by dIICf or dPCf), it was sufficient to calculate LCD to properly quantify the importance of habitat patches for dispersal fluxes into the habitat network. Accordingly, we recommend that conservation managers calculate only LCD in a first line approach, and then verify the degree of connection between large (high quality) habitat patches and the rest of the habitat

network before deciding whether the calculation of RD is required for quantifying the contribution of patches to dispersal fluxes at the scale of the landscape.

Concerning the role of habitat patches as stepping-stones, i.e. facilitating species dispersal between far habitat patches, the choice of RD or LCD could depend on the assumptions about how the species population functions. Considering the presence or absence of the linkage, i.e. the use of binary indices (BC, dIICc), almost all linkages were established for LCP above a certain dispersal distance of the species. In one study on a plant species (Neel 2008), IIC tended to explain genetic differences between populations better than PC, but for a Euclidean distance less than 2500 m, so actually a much shorter distance than in our study. If we hypothesize that one individual would be sufficient to change the genetic structure of population (see Wang 2004), the convergence of patch prioritization based on LCD and on RD should be expected. LCD indicated the minimum distance a particular individual had to move between habitat patches, and when the individual dispersal capacity was at least LCD, the individual was able to move to any population patch. Accordingly, our results show that the calculation of RD did not provide any further information about key stepping stones in the landscape.

When considering the linkage probability between habitat patches (dPCc), strong differences remained whatever the dispersal distance. RD considered the probability of dispersal between habitat patches taking into account path redundancy, i.e. it indicated the resistance distance one species moved between population patches (Fletcher et al. 2014). RD can be more closely correlated with genetic distance compared with LCP, which implies that taking into account the flux of dispersers better reflects genetic differences between populations than considering one (best) disperser (McRae and Beier 2007). Consequently,

we can hypothesize that RD-based dPCc predicts functional connectivity between populations better than LCD-based dPCc, since the establishment of linkages between patches is proportional to the number of dispersers, and not only to the inter-patch distance (Fletcher et al. 2014). The current map (Fig. S4) illustrates the differentiation of narrow corridors for forest species dispersal (pinchpoints), versus large corridors or alternative paths between habitat patches that increase the probability of dispersal for the species (compare dispersal probability in Figs 7a and 7b).

Future studies will use genetic data to corroborate that RD best identifies key landscape elements that contribute to the long-term persistence of species. Our results also show that LCD-based dPCc allowed the identification of landscape parts that remain difficult to reach for one individual because of a strong impedance of the surrounding landscape: restoration actions to facilitate individual dispersal will ameliorate the connectivity with other landscape parts, and probably also the long-term persistence of the species. Habitat patch importance was evaluated similarly according to RD based on 700-m corridor cut-off and 4000-m corridor cut-off, but if RD was calculated considering the entire surrounding landscape as space for dispersal movements, the prioritization differences between LCD and RD might be accentuated. Our results suggest that resistance-based connectivity is substantially affected by different conceptual approaches and not only by the way resistance values are parameterized (Mateo-Sanchez et al. 2015). Importantly, these approaches do not replace species monitoring or genetic studies nor finer-scaled investigations before protection or restoration actions are attempted.

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Table 1

Table 1. Binary and probabilistic connectivity indices used for prioritization of habitat patches in our study

	INDEX	TYPE	MEANING	REFERENCES
BC	Betweenness Centrality	Binary	Considers the role of patch <i>i</i> as connecting other patches (stepping-stone) with shortest pathways	Estrada and Bodin 2008; Bodin and Saura 2010
dIIC	delta IIC	Binary	Importance of patch <i>i</i> according to Integral Index of Connectivity. IIC considers both habitat amount and habitat reachability in habitat network, and linkages as dispersal events between patches. dIIC quantifies the loss of connectivity if patch <i>i</i> is removed from habitat network and can be decomposed into dIICf, dIICc, dIICi	Urban and Keitt 2001; Pascual-Hortal and Saura 2006; Saura and Rubio 2010
dPC	delta PC	Probabilistic	Importance of patch <i>i</i> according to Probability of Connectivity. Like IIC, PC considers both habitat amount and habitat reachability in habitat network, but the probability of dispersal between patches. dPC can also be decomposed into dPCf, dPCc, dPCi	Saura and Pascual-Hortal 2007; Saura and Rubio 2010
dIICf dPCf	Flux fraction of dIIC of dPC	Binary Probabilistic	Quantifies the role of patch <i>i</i> as receiving (emitting) flux from (to) other patches. It considers the attributes of <i>i</i> and of other patches, and the shortest pathways between them	Saura and Rubio 2010
dIICc dPCc	Connector fraction of dIIC of dPC	Binary Probabilistic	Quantifies the role of patch <i>i</i> as connecting other patches (stepping-stone). It considers shortest pathways passing through <i>i</i> and the attribute of other patches	Saura and Rubio 2010; Gurrutxaga et al. 2011; Saura et al. 2014
dIICi dPCi	Intra fraction of dIIC of dPC	Binary Probabilistic	Quantifies the role of patch <i>i</i> as providing intra-connectivity so considering only the attribute of <i>i</i> .	Saura and Rubio 2010

Figure Captions

Figure 1. Correlation between habitat patch importance according to LCD-based and RD-based index for binary (a) and probabilistic indices (b) for Sub-region. Intra fraction (i), flux fraction (f) and connector fraction (f) are the partition of node importance dIIC and dPC. Tick marks without labels are 700, 1000 and 6000 m respectively.

Figure 2. Relative contribution of each fraction intra (i), flux (f), connector (c) to habitat network connectivity according to LCD-based and RD-based indices for Sub-region. Each fraction represents the contribution of all individual habitat patches relative to their total importance for maintaining connectivity. Tick marks without labels are 700, 1000 and 6000 m respectively.

Figure 3. Habitat patch importance rank according to LCD-based versus RD-based indices for Sub-region. The higher the patch importance, the higher the rank. Minimal rank is attributed when several importance values are the same. Other dispersal distances are not shown. Circles illustrate some cases where prioritization strongly differed.

Figure 4. Among the 25 top-ranked habitat patches, number of patches identified by both LCD-based and RD-based indices.

Figure 5. Map showing the 25 top-ranked habitat patches according to dIICc for a maximum dispersal distance of 1000 m. Top-ranked patches only by RD-based (green), only by LCD-based (orange) and by both indices (lilac), other habitat patches in grey. Difference between LCD-based rank and RD-based rank in bold. Linkages are established when $RD \leq 1000$ m (red and green); and in fewer cases when $LCD \leq 1000$ m (red). Numbered arrows indicate three typical cases resulting from the difference in patch prioritization (see Results).

498 **Figure 6.** Maps showing the 25 top-ranked habitat patches according to dPCc for the 6000-m
499 median dispersal distance. LCD-based (a) and RD-based linkages (b) are represented
500 according to their dispersal probability. See Fig. 5 for other details.

501 **Figure 7.** Maps showing the 25 top-ranked habitat patches according to dPCc for the 25-km
502 median dispersal distance. LCD-based (a) and RD-based linkages (b) are represented
503 according to their dispersal probability. See Fig. 5 for other details.

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Figures

Figure 1

Figure 2

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511 **Figure 3**

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Figure 5

520 **Figure 6**

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Supporting Material Captions

- Figure S1.** Correlation between habitat patch importance according to LCD-based and RD-based index for binary and probabilistic indices for Region.
- Figure S2.** Relative contribution of each fraction intra, flux and connector to habitat network connectivity according to LCD-based and RD-based indices for Region.
- Figure S3.** Habitat patch importance rank according to LCD-based versus RD-based indices for Region.
- Figure S4.** Current intensity map represented areas with high density of dispersal flux, taking into account alternative paths for Sub-region.

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